# WEB MANIPULATION AND TWO STEREOTYPED ATTACK BEHAVIORS IN THE OGRE-FACED SPIDER DEINOPIS SPINOSUS MARX (ARANEAE, DEINOPIDAE)

# Jonathan Coddington

Department of Entomology National Museum of Natural History Smithsonian Institution Washington, DC 20560, U.S.A.

and

# Claudia Sobrevila

Department of Botany National Museum of Natural History Smithsonian Institution Washington, DC 20560, U.S.A.

### **ABSTRACT**

This study shows that *Deinopis spinosus* Marx has at least two stereotyped attack behaviors, each elicited by different stimuli. In "backward" strikes the spider expands the net backward over its cephalothorax and away from the substrate; these strikes capture aerial prey. Vibratory stimuli are sufficient to elicit backward strikes. In "forward" strikes the spider expands the web downward and forward against the substrate; these strikes capture walking prey, and visual rather than vibratory stimuli are more effective. We describe the mechanisms underlying each type of strike and the extraordinary extensibility of the web.

# INTRODUCTION

Very few web-spinning spiders actively manipulate their webs to intercept prey. The uloborid genus *Hyptiotes* Walckenaer and the araneoid family Theridiosomatidae tense their webs and release them suddenly after prey strike the web (McCook 1889; Opell 1982; Coddington 1986a), but they do not actively move the webs to intercept near-flying prey. The bolas spiders (*Mastophora* Holmberg and related genera) swing or twirl a tethered viscid silk ball toward near-flying moths (Eberhard 1980, Stowe 1986). All of these spiders catch only aerial prey, whether they manipulate the web in advance or not, and none of them have more than a single stereotyped technique of web manipulation. We report here on a web-spinning spider, *Deinopis spinosus* Marx, that not only actively manipulates its web to intercept prey, but also uses it in at least two distinct attack behaviors—one to catch aerial prey, and one to catch walking prey.

The circum-Caribbean *Deinopis spinosus* belongs to the tropical family Deinopidae, often called "ogre-faced spiders". All deinopids spin architecturally

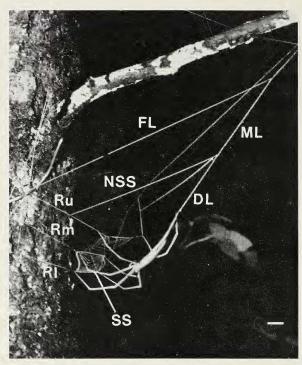


Fig. 1.—Deinopis spinosus in prey ready postures. Note 4th legs gripping dragline (DL) attached to midline (ML), 3rd legs on upper radii (Ru), 2nd legs on middle radii (Rm), 1st legs on lower radii (Rl). Legs control the sticky silk portion (SS). Note frame lines (FL) and persistent segments of non-sticky spiral (NSS). Compare this view with Fig. 5. Scale = 1 cm.

uniform, highly specialized webs (Fig. 1). The webs may be called specialized because analysis of the detailed motor patterns used to construct the web shows that they are derived phylogenetically from the classic orb-web, an architecture otherwise found only in the Uloboridae and within the superfamily Araneoidea (Coddington 1986b). The form of deinopid webs is unique to the family, and ever since its discovery (Ackerman 1926) has intrigued and attracted biologists. The web is small compared to the size of the spider, and unless the prey caught are very small (Robinson 1977, 1983), each successful capture usually causes the destruction of the web; to catch more prey, the spider must spin a new web.

Other aspects of deinopid behavior also appear to be fairly uniform throughout the family. All deinopid species observed to date, for example, grasp the corners of the sticky portion of the web with their first two pairs of legs while motionless in their prey-ready posture (Fig. 1), and then simultaneously lunge and push the expanded web as much as 1-2 body lengths away to ensnare prey (Menneus camelus Pocock, Ackerman 1926; M. unifasciatus (L. Koch), Austin and Blest 1979; Deinopis subrufus L. Koch, Baum 1938, Roberts 1954, Austin & Blest 1979; D. spinosus, Theuer 1954; D. longipes F. O. Pickard-Cambridge, Robinson and Robinson 1971). However, the two most detailed studies to date on Deinopis species (Theuer 1954; Robinson and Robinson 1971) differ in their conclusions about the manner in which the web is used, and something of a controversy has developed as to whether they strike forwards against pedestrian prey, or backward toward aerial prey.

A subsidiary mystery (Eberhard, pers. comm. and authors cited above) is the amazing extensibility of the deinopid web. During any strike the web area may expand 10x (compare Figs. 2a, d; 3a, d), which rivals the record for any spider silk (Denny 1976).

This paper seeks to answer 3 questions. (1) Does *D. spinosus* use backward strikes, forward strikes, or both? (2) Can the releasing stimuli for the strikes be elucidated experimentally? (3) How exactly does either kind of strike occur, and how does the architecture of the web and the behavior of the spider enable the strike?

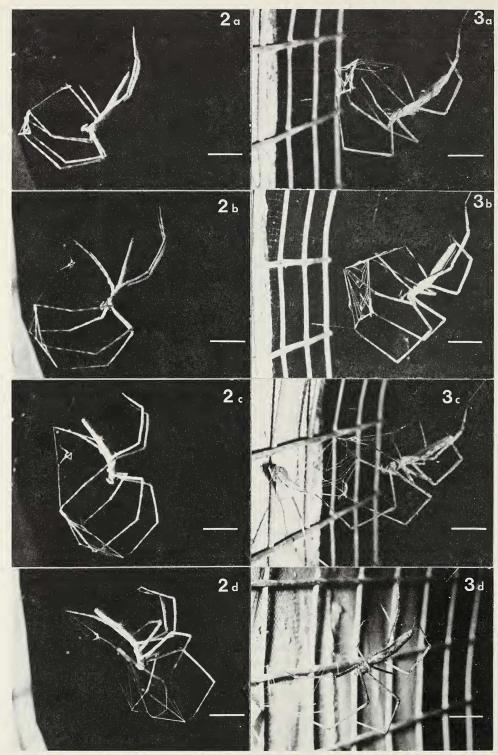
# MATERIALS AND METHODS

Web construction and predatory behavior were observed in 19 D. spinosus females for a total of 52 hours in outdoor but caged situations, and in 28 individuals for a total of 17 hours in natural field conditions in Gainesville, Florida during August, 1985. Spiders were illuminated with 6 volt headlamps masked with dark red gel filters (no transmittance below 600 nm). In both cages and field we noted web-substrate distances, activity times, and documented preyready postures, web placements, and aspects of construction behavior with still photographs. We described all natural predatory strikes seen and also attempted to elicit predatory strikes with various natural and artificial stimuli.

In order to determine the different kinds of strikes used by *D. spinosus* to intercept prey, we elicited predatory strikes with stimuli presented by six means: a vibrating tuning fork held adjacent to the web; audibly humming next to the web; paper models mounted on wires; dead insects mounted on wires; tethered flapping or motionless live prey held adjacent to the web; and releasing live prey into the cages and observing subsequent events. Qualitatively different strikes were characterized by presence or absence of motion patterns during the strike, and by qualitatively different orientations of the web during the strike. We made no attempt to measure quantitative variation in leg extension, body movement, or web orientation. A "strike" was judged to have occurred during a stimulus presentation if the strike occurred within 0.5 sec of the stimulus.

The tuning fork experiments tested if a vibratory stimulus (acoustic or near-field air movement) would elicit a strike. The fork (256 Hertz), either vibrating or not according to the odd-even sequence of a series of random numbers, was presented 36 times to each of nine spiders. In all presentations the animals therefore received the visual stimulus of the tuning fork as a control, but only in some did they receive a vibratory stimulus as well. The tuning fork was positioned behind the spider at a distance of 3-5 cm. The occurrence or absence of a strike was noted, and the fork then removed for about 5 seconds before the next trial. In each presentation of a vibratory stimulus, an effort was made to present roughly the same level of energy.

The vocal humming experiments tested the efficacy of acoustic stimuli in the absence of visual stimuli. A series of 11 "hums" were presented to each of four individuals in the following manner. The observer positioned him or herself ca 30 cm to the side of the web and spider, and emitted at 10 sec intervals a low-pitched hum with the lips closed.



Figs. 2-3.—Stop-action sequences of backward and forward strikes. All photographs are from different strikes, and some may be during web contractions, not extension. Fig. 2, Backward strike: a. prey-ready posture; b. 1st legs moving backward; c. body rotates; d. almost maximum extension (note partly flexed 1st and 2nd legs). Fig. 3, Forward strike: a. prey-ready posture; b. 1st legs extend downwards; c. 4th legs allow movement toward substrate, 1st legs extend further, note moth on wire as lure; d. 2nd legs extended, 1st partly withdrawn. Scales = 1 cm.

Tensions in lines were measured with fine glass filaments used to deflect web lines specified amounts and then later calibrated with known weights (Opell 1985).

# **RESULTS**

Web heights in the field averaged 148 cm (range = 49-300) from the ground. Without exception (n = 28, e.g., Figs. 1, 5) webs were constructed so that the approximately 1 cm square sticky portion was within 1-3 cm of a broad (at least 10 cm) roughly vertical substrate (e.g., tree trunk, palmetto leaf, wooden post). Webs could be found from about 2000 (1 hour after sunset) until at least 0300. No webs were seen during daylight hours under either natural or captive situations. Caged spiders built at roughly the same time as uncaged spiders and the morphology of the webs (n = 65) was indistinguishable. We saw no consistent differences in construction behavior, prey-ready postures, or attack behavior between individuals in cages and those in natural habitats. Our use of dim red light to observe spiders did not seem to perturb spiders in either field or caged situations.

We observed 22 strikes against live prey, and 119 strikes in response to artificial stimuli, totalling 141 instances of attack behavior. All observed strikes were stereotyped, either backward (n = 121) or forward (n = 20) strikes, as described below. In numerous cases, the spiders followed strikes against artificial stimuli with prey wrapping behavior, the normal sequence of actions in deinopid predation (Robinson & Robinson 1971). Thus, the spiders did not seem to be using either strike in a non-predatory behavioral context, such as defensive behavior against a threatening stimulus.

Description of backward strikes.—We call the strike used by *D. spinosus* to catch aerial prey a "backward" strike. During the strike (Figs. 2a-d) the spider retains its grip on the dragline with its 4th legs, rotates the body backward in space, and bends the 1st and 2nd pairs of legs outward and backward past the cephalothorax. In successful backward strikes the prey may be entangled on either surface of the sticky silk sheet, thus caught either on the outward or inward motion of the sheet.

Description of forward strikes.—D. spinosus uses a downward, forward strike to catch walking prey on the substrate in front of the web (Figs. 3a-d). We name this a "forward" strike. The animal spreads and extends its 1st and 2nd pairs of legs laterally and frontally, thus expanding the net. A major difference between backward and forward strikes lies in the use of the 4th legs. In forward strikes, the 4th legs allow the dragline to slip rapidly between the claws. The increased length of the dragline allows the spider and expanding web to drop down and forward, pivoting about the upper radius/non-sticky spiral junction and radial attachments to the substrate (Fig. 1, Ru - NSS, Rm, R1) until the front four tarsi of the spider contact the substrate (Fig. 3d).

Mechanism of backward strikes.—During the very brief duration of a backward strike (Fig. 2), the spider's body basically rotates in place rather than moving a substantial distance, as in a forward strike. The forces required to expand and move the web backwards all seem explicable by leg movements of the spider. The contraction of the 4th legs, and the rotation of the body, 1st legs, and 2nd legs downward and backward expands the sheet of the web and moves it about the positions of the 3rd legs, which remain relatively motionless.

Table 1.—Backward strike responses by different spiders to tuning fork vibrations and vocal humming. N = total number of stimulus presentations. \* = P < 0.01; \*\* = P < 0.001. Tests of individual and pooled responses each had one degree of freedom (df); tuning fork heterogeneity, 8 df; vocal heterogeneity, 3 df.

TUNING FORK					VOCAL HUMMING				
Individual	N	No Vibration	Vibration	G-test	Individual	N	Humming	No Humming	G-test
1	18	1	0	n.s.	10	11	8	0	**
2	18	15	0	**	11	11	11	0	**
3	18	6	0	*	12	11	11	0	**
4	18	2	0	n.s.	13	11	10	0	**
5	18	16	0	**					
6	18	3	0	n.s.					
7	18	6	0	*					
8	18	8	0	**					
9	18	2	0	n.s.					
TOTAL	162	59	0	**	TOTAL	44	40	0	**
HETEROGENEITY				**					n.s.

Mechanism of forward strikes.—The rapid movement of the spider's body towards the substrate during a forward strike (Fig. 3) is powered at least in part, and probably primarily, by gravity. It is possible that the spider pulls on the radii to increase its velocity or to guide its trajectory. Measurements of tensions in the uppermost segments of web midlines (Fig. 1, ML) average 45% more than the spider's body weight (n = 5), but the tensions in frame lines (Fig. 1, FL) average 35% less (n = 3). Given the geometry of the prey-ready posture (Fig. 1), these magnitudes of tensions would be unlikely to contribute in a major way to the spider's acceleration toward the substrate. Instead, the geometry resembles more a concentrated weight hanging on a lax line (Merriam 1975). Such a cable system cannot act as an efficient "catapult". However, if the spider pulled in on the upper radii (Fig. 1, Ru) with its 3rd legs, it probably could increase its acceleration toward the substrate. Letting the midline slip between the 4th leg claws would still be a necessity.

Elicitation of backward strikes.—Backward strikes were easily elicited with a tuning fork or by humming, and the results of these more controlled experiments are reported below. We also used insect prey (moths, mosquitos, tabanids, tipulids, *Drosophila*) to elicit 14 backward strikes in 19 presentations to a total of 10 spiders. Ten successful elicitations involved freely flying prey (including one unstaged, "natural" strike observed in the field against a tipulid) and four involved flapping prey held by one wing with forceps. Two of the five unsuccessful presentations occurred when motionless (i.e., non-flapping or non-flying) prey were used (predictably inappropriate stimuli). Three occurred during one course of presentations to an apparently unresponsive spider.

In both field and caged animals, the occurrence of a backward strike was highly dependent on vibratory stimuli. In the field, three tuning fork presentations to each of three animals yielded eight backward strikes (not included in Table 1), but many presentations of non-vibrating tuning forks to field animals never elicited a response.

In caged animals, Table 1 shows that mere visual presentation of the tuning fork to caged animals is also completely ineffective in eliciting backward strikes

(none of 162 tries). However, the occurrence of backward strikes was highly dependent on the presentation of a vibratory stimulus (P < 0.001, Table 1). The efficacy of a vibratory stimulus in eliciting backward strikes varies significantly among individuals (G of heterogeneity: P < 0.001, Table 1). Lastly, animals accommodate significantly to repeated presentations (28 backward strikes summed over all animals in the first six presentations versus 12 strikes in the last six; Chi-square = 10.52, P < 0.01).

The above results suggest that a vibratory stimulus is necessary, but do not show that it is sufficient because the animals received a visual stimulus as well. As nearly as possible, the humming experiments presented only an acoustic or vibratory stimulus to the spiders, and successfully elicited backward strikes (P < 0.001, Table 1). Although it was more difficult to standardize a humming stimulus than the tuning fork, the results are highly significant and show that a vibratory stimulus is indeed sufficient.

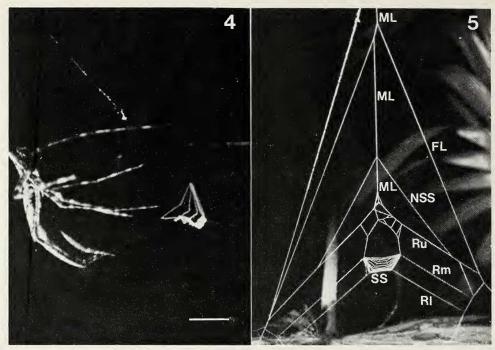
Elicitation of forward strikes.—Experimental elicitation of forward strikes using artificial stimuli proved difficult. Vibrations applied to substrate beneath the web or to web strands were ineffective. The Robinsons (1971) were able to elicit four strikes against shadows projected on cage walls in front of the webs of D. longipes, but this stimulus was ineffective with D. spinosus. However, we were able to elicit 12 strikes in 12 presentations to two spiders using small paper models (n = 4) or dead insects (n = 8) mounted on wires (as in Fig. 3c). These results support the inference that visual stimuli are essential to release forward strikes, but the use of dead insects as stimuli might also have provided olfactory cues.

We also saw eight forward strikes against live prey by five spiders. In six instances, three spiders used forward strikes to ensnare termites walking beneath the web, and in two additional instances, two spiders used forward strikes to catch a tethered moth and juvenile cricket.

Web construction as it relates to attack behavior.—The final stages of web construction were observed 12 times and the motion patterns are quite stereotyped. During sticky spiral construction (Fig. 4), the spider is head up with respect to the web, but after completion of the sticky spiral, the spider turns head down, attaches its dragline to the midline (Figs. 1, 5), grasps the web with its four front tarsi, and cuts the lowest midline segment (Fig. 5). The grip of the fourth legs keeps the spider and sticky portion of the web from falling toward the substrate. The spider then lets dragline slip through its fourth tarsi, falls slowly downward, and taps forward and downward with its first legs to contact the substrate (Fig. 6). Finally the fourth legs reel in dragline as the first legs again take up the bottom corners of the sticky web, thus raising spider and web up and away once more from the substrate, and into the prey-ready posture (Fig. 1).

These operations are critical to web function for two reasons. First the cutting of the middle portion of the midline enables the web and spider to fall forward toward the substrate. Second, the attachment of the dragline to the upper midline allows the spider to adjust its distance from the substrate and to control its fall towards the substrate during a forward strike. Third, the final tapping motions (Fig. 6) allows the spider to orient with respect to the substrate, and apparently to gauge distance, immediately before assuming a prey-ready posture.

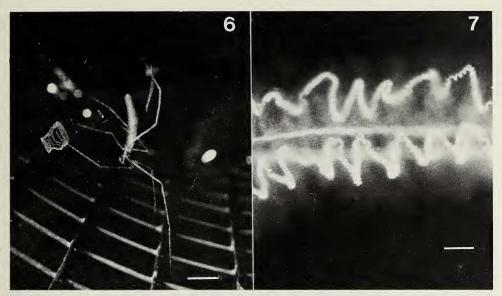
Sticky silk extensibility.—Examination of sticky spiral construction (n = 16) and web samples on slides shows that a hypothesis of extremely extensible silk



Figs. 4-5.—4, Deinopis spinosus constructing sticky spiral. Note the length of the current sticky silk segment; 5, Incomplete D. spinosus web showing lowest midline segment not yet removed and incomplete sticky spiral. Abbreviations: midline (ML); frame line (FL); non-sticky spiral (NSS); upper radius (Ru); middle radius (Rm); lower radius (Rl); sticky silk (SS). Scales = 1 cm.

(and thus extraordinary material properties) may not be necessary to explain the ability of the sticky web to expand tremendously. Only the non-sticky radii or the sticky silk segments could potentially resist the efforts of the spider to spread the web. However, *D. spinosus* usually cuts the attachments of the middle and lower radii to each other and of all of these to the upper radii (Figs. 1, 5). These non-sticky lines therefore do not impede expansion of the catching portion of the web, though they do resist the movement of the web as a whole during a backward strike. The upper radii, which do remain attached to each other even after the midline is cut to produce the finished web (Fig. 1), also do not resist the expansion of the web because the expansion is due mainly to movement of the 1st and 2nd pairs of legs which hold the middle and lower radii.

Therefore, the only silk which might constrain web expansion is the sticky silk itself. However, the spider holds its spinnerets well away from the web while it spins the cribellar spiral so that each segment of sticky silk is actually spun longer than its apparent length in an unexpanded web (Fig. 4). In a sense, the spider spins each sticky silk segment at or near its expanded length, only to contract it immediately before final attachment. Examination of sticky silk collected in the contracted state (Fig. 7) shows that it is composed of four components: a doublet of parallel fibers, a mass of much finer paracribellar fibers associated with the straight fibers, a doublet of helically coiled fibers, and a cloud of puffed cribellar silk. The helical fibers confirms that the cribellar silk lines are indeed highly contracted. When one of these complex sticky lines is slowly stretched, the straight fibers snap at about 150% extension, but the helical fibers and the cribellate silk stretch much farther. Thus the remarkable extensibility of deinopid



Figs. 6-7.—6, *Deinopis spinosus* tapping downward to locate substrate before assuming ready posture. Scale = 1 cm; 7, Photomicrograph of *D. spinosus* sticky silk in contracted state. Note spiralled fibers. Scale = 0.05 mm.

webs seem adequately explained by particular behaviors during the process of construction.

# DISCUSSION

Our results demonstrate two different stereotyped attack behaviors in D. spinosus, and resolve a controversy in the literature between Theuer (1954) and Robinson and Robinson (1971). Theuer stated: (1) that D. spinosus expands the web with its first two pairs of legs, backward over its carapace and away from the substrate in front of the web; (2) that it "could in no way be construed to be a hurling forward and the throwing down of the net over an insect..." (p. 28); and (3) that "since the entire structure is in one plane and the spider itself does not hold on to any point in another plane, it appears an obvious physical impossibility that either spider or snare can go forward or backward [in space]" (p. 28). The strike described by Theuer seems to be what we call a backward strike, and he also pointed out that it would be effective only against jumping or flying prey. He concluded prior observers of deinopid behavior had been wrong in reporting downward and forward lunges, perhaps because he thought such behavior was physically impossible.

On the other hand, the Robinsons (1971) described in a different species, D. longipes, a behavior very similar to what we call a forward strike and pointed out: (1) that Theuer's observations did not agree with theirs or those of any other workers (Ackerman 1926; Baum 1938; Roberts 1954); (2) suggested that Theuer's observations had been based on a false assumption (that neither spider or snare can go forward or backward in space); and (3) questioned Theuer's claim that the kind of strike he described could be effective or frequent.

Our results with D. spinosus tend to corroborate some points and refute other points made by these two previous studies. Theuer apparently missed entirely the

occurrence of forward strikes in *D. spinosus*, but he did describe accurately a type of strike which catches aerial prey effectively. The skepticism of the Robinsons concerning the ability or likelihood of deinopids in general to catch aerial prey with backward strikes, on the other hand, seems to be unfounded, although very possibly *D. longipes* does not. Certainly they saw no aerial prey captured, and despite much experience with the species, saw only forward strikes. Theuer was wrong about the inability of a deinopid to move its center of mass during a strike, and the Robinsons may have underestimated the role of fourth legs and gravity in their explanation of how a forward strike occurs, at least judging by our observations on *D. spinosus*. Interestingly, Ackerman (1926) and McKeown (1963) also mention deinopids catching aerial prey, and Austin and Blest (1979) elicited what apparently was a backward strike in *D. subrufus* in response to a clearing of the throat.

Alternative explanations for the mechanics of forward strikes do exist in the literature. Baum (working on D. subrufus) said that the radii of the web were under extreme tension, and that if the fourth legs of the spider released the dragline (Fig. 1, DL), the elastic force in the radii would "catapult" the spider and web forward against the substrate. That all extant photographs of deinopids in ready postures show them in lax catenaries would seem to invalidate that hypothesis at the outset. The Robinsons (1971:92, working on D. longipes) speculated that"...this movement, presumably, is possible because of the elasticity of the silken web members to which it [the web] is attached. It is more difficult to see what the spider pushes against in order to make the strike. The hackled threads of the net attachment are certainly more elastic than the silk of the supporting framework and this lower elasticity, plus the inertia of the spider's body, presumably makes the lunge possible." We would agree that deinopids have nothing to push against, but see a lesser role for elasticity, either of the sticky or non-sticky threads, in powering a forward strike. Our observations suggest that in D. spinosus a forward strike is powered mainly by gravity, but possibly to a subsidiary extent by pulling on the web scaffolding.

One possible reason for the lack of agreement in the literature is that Theuer and the present authors worked on *D. spinosus*, the Robinsons on *D. longipes*, Baum and Roberts on *D. subrufus*, and Ackerman on *Menneus camelus*. However, our research on building behavior in *D. spinosus* (unpubl.) and *Deinopis* sp. (Coddington 1986b) shows a high degree of stereotypy among species, and from that lack of variation in one stereotyped pattern we are inclined to suggest that the genus *Deinopis* shows little diversity in mechanism of attack behavior.

The tuning fork experiments show that both visual and vibratory stimuli together will release backward strikes, and the humming experiments show that vibration alone is probably sufficient. No kind of visual model, nor any of the motionless prey presented to *D. spinosus*, elicited backward strikes, thus corroborating the tuning fork data that visual stimuli alone will not elucidate a backward strike. On the other hand, we were able to elicit forward strikes experimentally with models and mounted insects, mainly visual stimuli, and in their study, the Robinsons (1971) reported that shadows of small round balls projected beneath the web elicited forward strikes from *D. longipes*, also suggesting that visual rather than vibratory cues, are important. Other evidence also strongly implies that visual stimuli are important in eliciting forward strikes.



Fig. 8.—Deinopis spinosus "ogre" face. The large eyes are the posterior medians. Scale = 0.5 mm.

Deinopids have posterior median eyes which are probably the largest simple ocelli in arthropods (Fig. 8). With focal lengths of about 0.8 mm and f-numbers of 0.58, they can see in about 1/12 the illumination required by humans, and possess specialized physiological mechanisms to ensure low light sensitivity (Blest 1978; Blest and Land 1977). The resolution of deinopid eyes, on the other hand, is relatively poor (Blest and Land 1977).

The elicitation results do make biological sense. If deinopids see well at night, one would expect that they would use forward strikes on walking prey which they can see, but not "hear." Walking prey very likely impart only the slightest vibrations to the spider, and indeed some spiders spin webs attached to vines rather than directly to the substrate towards which the web is always oriented, and on which prey would move. The bulk of aerial prey, of course, that deinopids would encounter would present both visual and vibratory stimuli. Perhaps only spiders on draglines might be a case of "aerial" yet non-vibratory prey, but given the orientation of the deinopid web, spiders on draglines susceptible to backward strikes seem unlikely. The characteristic femoral trichobothria are likely receptors for near-field air vibrations (B. D. Opell, pers. comm.).

Prey records for deinopids were reviewed and augmented by Austin and Blest (1979). Without doubt, most records are of walking prey. Their own data on 84 prey of *D. subrufus* and *Menneus unifasciatus* suggest that the vast majority were walking, but they do mention a population of *D. subrufus* in Queensland whose main prey items were tipulid flies, and we saw *D. spinosus* ensnare a flying tipulid with a classic backward strike. Nevertheless, the available data clearly affirm that walking prey are more important than flying prey in the diet of deinopid species studied thus far.

The tuning fork experiments also documented significant accommodation to vibratory stimuli in individuals, and significant differences between individuals.

Most animals accommodate to prolonged or repeated exposure of stimuli, and certainly presentation of vibratory stimuli every 5 seconds is a fairly frequent schedule. These results, however, also argue for the effectiveness of vibration as an important component of the releasing stimulus, simply because the response tended to disappear with repeated exposure to vibrations.

Peters (1984) studied the fine structure of uloborid sticky silk, but found only three components: puffed cribellar silk, massed paracribellar fibers, and a doublet of pseudoflagelliform fibers. Uloborids are possibly the sister group of deinopids (Coddington, 1986b, c), and thus should be a good model for interpretation of deinopid sticky silk fine structure. However, deinopid silk exhibits an extra pair of axial fibers. One pair of axial fibers presumably issues from pseudoflagelliform glands, and the other from either major or minor ampullate glands, but it is difficult to say which at this point.

Finally, the extensibility of the web may not be due to any particular ability of the silk itself, but instead to a beautifully functional series of behaviors operating during the process of web construction. That the spider constructs long sticky silk segments and then contracts them seems almost more elegant a solution to the conundrum of the web's extensibility than arcane material properties. One wonders whether the spider precisely adjusts the length of each segment to its role in the extended web during the brief moment of a strike, but such behavior would argue for a degree of functional precision that seems unlikely. Still, the possibility exists, and with recording equipment could be tested. We already know that deinopid webs hold many surprises, and no doubt more remain to test our credulity.

### ACKNOWLEDGMENTS

A Research Opportunities Fund Grant from the Smithsonian Institution to the senior author funded the behavioral research in Gainesville. We would like to thank Francis E. Putz and Michelle N. Holbrook for their hospitality, logistical support and the use of their porch; Edwin J. Conklin, Donald Younker, and Randall Brown of the State of Florida Department of Natural Resources for permission to conduct research at the Devil's Millhopper State Park; M. K. Stowe for suggesting the Millhopper as a study site; and W. G. Eberhard, B. D. Opell, M. H. Robinson, and M. K. Stowe for their excellent suggestions on improving the manuscript.

### LITERATURE CITED

Ackerman, C. 1926. On the spider, *Menneus camelus* Pocock, which constructs a moth catching expanding snare. Ann. Natal. Mus., 5:411-422.

Austin, A. D. and A. D. Blest. 1979. Biology of two Australian species of dinopid spider. J. Zool. London, 189:145-162.

Baum, J. 1938. On the habitats of the Australian spider *Dinopis subrufus* L. Koch. Vestnic Ceskoslovenske Spolecnosti Zoologicke, 5:28-33.

Blest, A. D. 1978. The rapid synthesis and destruction of photoreceptor membrane by a dinopid spider: a daily cycle. Proc. R. Soc. London (B), 200:463-483.

Blest, A. D. and M. F. Land. 1977. The physiological optics of *Dinopis subrufus* L. Koch: a fish-eye lens in a spider. Proc. R. Soc. London (B), 196:197-222.

Coddington, J. A. 1986a. The genera of the spider family Theridiosomatidae. Smithsonian Contrib. Zool., 422:1-96.

Coddington, J. A. 1986b. Orb webs in "non-orb weaving" ogre faced spiders (Araneae: Dinopidae): a question of genealogy., J. Cladistics, 2:53-67.

Coddington, J. A. 1986c. The monophyletic origin of the orb web. Pp. 319-363, In Spiders-Webs, Behavior, and Evolution. (W. A. Shear, ed.). Stanford Univ. Press, Stanford.

Denny, M. 1976. The physical properties of spider's silk and their role in the design of orb-webs. J. Exp. Biol., 65:483-506.

Eberhard, W. G. 1980. The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneae), Psyche 87:143-169.

Merriam, J. L. 1975. Statics, 2nd. Ed., SI Version, 381 pp. John Wiley & Sons, New York, NY.

McCook, H. C. 1889. American Spiders and their Spinningwork, vol. 1. Acad. Nat. Sci. Philadelphia. (publ. by the author), Philadelphia.

McKeown, K. 1963. Australian Spiders. Angus & Robertson, Sydney.

Opell, B. D. 1982. Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). J. Arachnol., 10:185-191.

Opell, B. D. 1985. Web monitoring forces exerted by orb-web and triangle-web spiders of the family Uloboridae. Canadian J. Zool., 63:580-583.

Peters, H. M. 1984. The spinning apparatus of Uloboridae in relation to the structure and construction of capture threads (Arachnida: Araneae). Zoomorphology, 104:96-104.

Roberts, N. L. 1954. The Australian netting spider, *Dinopis subrufus*. Proc. Roy. Zool. Soc. New South Wales, 54:24-33.

Robinson, M. H. 1977. Tropical Spinners. New Scientist (Dec. 1, 1977).

Robinson, M. H. 1983. Neotropical arachnology: historic, ecological and evolutionary aspects. Proc. IX Latin American Congress of Zoology, Oct. 1983:89-100.

Robinson, M. H. and B. Robinson. 1971. The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge. Amer. Midland Natur., 85:85-96.

Stowe, M. K. 1986. Prey specialization in the Araneidae. Pp. 101-131, In Spiders-Webs, Behavior, and Evolution. (W. A. Shear, ed.). Stanford Univ. Press, Stanford.

Theuer, B. 1954. Contributions of the life history of *Dinopis spinosus*. Unpubl. MS thesis, Univ. of Florida. 74 pp.

Manuscript received April 1986, revised October 1986.